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THICK-WALLED ROOT HAIRS OF GLEDITSIA AND RELATED GENERA

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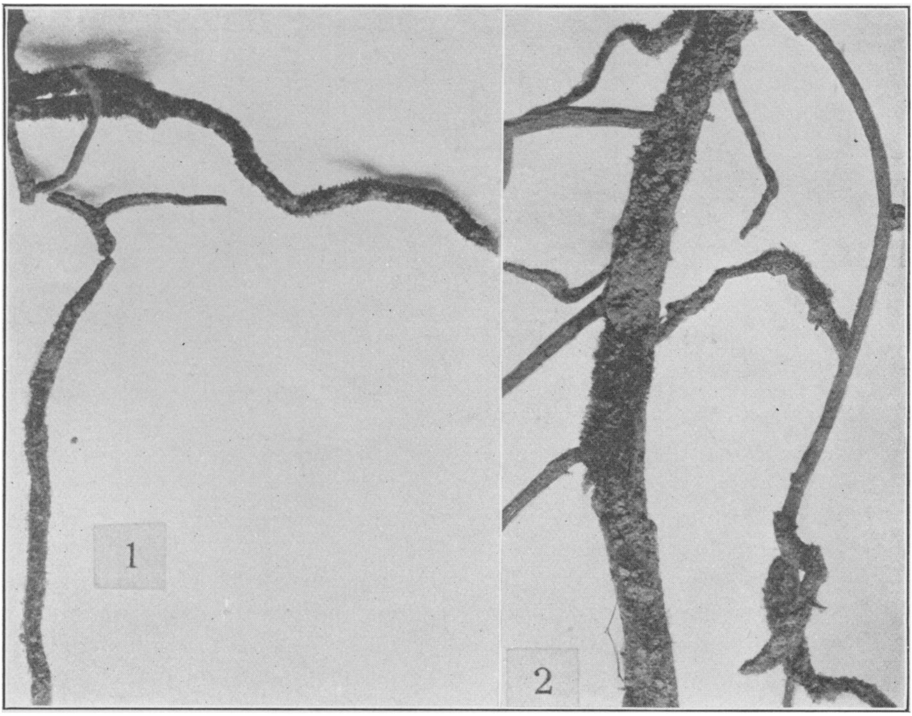
A few years ago my attention was called by the late Professor T. J. Burrill to the peculiar appearance of the surface roots of *Gleditsia triacanthos*, the honey locust, growing in the "Forestry" at the University of Illinois. These roots, which were abundant and easily obtained, when examined with the naked eye looked somewhat like ectotrophic mycorrhizas. It was noticed at once, however, that instead of the coral-like clusters of short, stubby roots characteristic of ectotrophic mycorrhizas the branching was normal, and the peculiar-appearing portion extended several inches back from the ends of the roots and in fact included practically all of the smaller parts of the root system. The color was rather dark brown. Under a lens



Figs. 1, 2. Roots of *Gleditsia triacanthos* covered with thick-walled root hairs.

these roots presented the appearance that is seen in figures 1 and 2: bristling with projections which I still thought to be due to a fungus. A cross section examined under the microscope, however, showed at once that these projections are thick-walled root hairs; figure 3 being a camera lucida drawing of one of these hairs. The actual thickness of the walls of these hairs, as measured with a Spencer Lens Co. screw micrometer, averages approximately 2 μ. This is about four times as thick as the walls of the root hairs of barley seedlings grown in petri dishes on filter paper. It is also about four times as thick as the walls of the newly formed hairs on the roots of honey locust seedlings grown in soil, as will be brought out later.

The hairs do not average very long, only about four tenths of a millimeter, but they are stiff and rigid and do not shrivel when exposed to the air. The photographs shown in figures 1 and 2 were taken from specimens that had lain unprotected on my desk for more than a month, during which time they had not shriveled in the least.

The chemical composition of the walls has not been determined. It is certain that chemical changes take place during the thickening of the walls, but repeated tests with phloroglucin and hydrochloric acid failed to detect any lignification while a cellulose reaction was finally obtained by allowing sections to remain in chloriodide of zinc solution for twenty-four hours. It has also been impossible to determine whether these hairs contain living protoplasm, for the walls are so thick and so dark-colored that it is not possible to see through them.

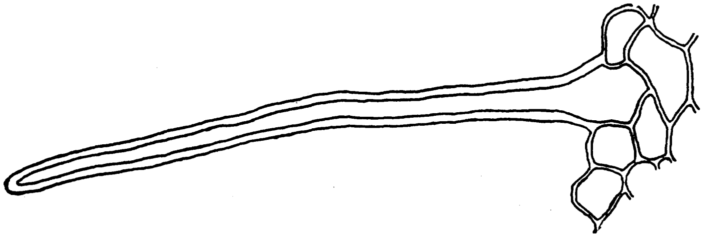


FIG. 3. A thick-walled root hair of *Gleditsia triacanthos*.

During the summer of 1919 I examined the roots of a large number of *Gleditsia triacanthos* trees in various localities and in very diverse habitats, the habitats ranging from the climax upland forest of Champaign county, Illinois, to the typical bottomland forests along the Vermillion River in Vermillion County, Illinois. To my surprise I found that the presence of thick-walled root hairs is a constant character of this species. I have not been able to find a honey locust tree on whose roots the hairs were not present in abundance. In order to determine whether the hairs are present on more than the superficial roots, a hole was dug near a honey locust tree in the "University Woods" (a sixty-acre tract of climax forest belonging to the University of Illinois and situated four miles northeast of Urbana, Illinois), and the roots were examined to a depth of four feet. Thick-walled root hairs were found as abundantly at that depth as near the surface. In some cases the smaller parts of the root system are completely covered with root hairs while in other cases there are patches which are entirely free from hairs. These latter are probably due to the fact that the movements of the roots in the soil due to growth often break off the hairs.

Early in February, 1920, some seeds of *Gleditsia triacanthos* were obtained and planted in the greenhouse. After seedlings had appeared, the root systems of some of them were examined at the end of one week, three weeks, four weeks, eight weeks, fourteen weeks, and twenty-one weeks. The following excerpts from my notes will serve as a report on this part of the work:

Feb. 17. Seedlings one week old. The root (tap root) is 7 cm. long and unbranched. It is abundantly covered with root hairs throughout its entire length. Near the tip these hairs are whitish or colorless and have very thin walls. They contain protoplasm and look very much like the root hairs of other plants. Toward the base of the root the hairs are becoming brown and the walls are somewhat thickened.

March 2. Seedlings three weeks old. The total height of the plant above ground is about 14 cm. The tap root is from 10 to 12 cm. long and has 10 to 15 branches varying from 1 mm. to 2 cm. in length. The entire root system is clothed with root hairs. The thickness of the walls of the oldest and brownest hairs is now about 0.95 μ, while the walls of the young hairs near the tips of the roots are only about 0.5 μ thick.

March 9. Seedlings four weeks old. The longest secondary root found at the age of three weeks was 2 cm. The longest at four weeks is 5 cm. These secondary roots, therefore, may grow as much as 3 cm. in a week, or more than 4 mm. per day. The youngest hairs are usually found about 4 to 5 mm. from the tip, while at 12 mm. from the tip the hairs are beginning to turn brown. Therefore, they probably remain colorless only about two days.

April 6. Seedlings eight weeks old. The thickness of the walls in the oldest hairs is now about 1.5 μ.

May 18. Seedlings fourteen weeks old. The walls of the oldest hairs have now reached the full thickness of approximately 2.0 μ. The epidermis has ruptured in several places on the older parts of the root system, and the root hairs have disappeared from parts.

July 6. Seedlings twenty-one weeks old. The entire length of the root system is now about 27 cm., and branches are numerous. Root hairs are present on most of the root system. They are very abundant as much as 15 cm. from the tips of some of the roots. On the first 7 or 8 cm. below the surface of the soil the epidermis has ruptured and many of the hairs have disappeared. Many still remain, however, even in this region, though they are often broken. There are other places on the root system where root hairs are entirely lacking, probably because of movements of the roots within the soil which break them off. It is apparent that in general the hairs remain for as long a time as the epidermis.

During the spring and summer of 1920 the roots of a number of trees of *Gymnocladus dioica* and *Cercis canadensis*, both of which are closely related to Gleditsia, were examined. It was found that both of these trees produce thick-walled root hairs similar to those of *Gleditsia triacanthos* but by no means so abundantly as in the latter species. In Cercis they are even less frequent and less evident than in Gymnocladus.

DISCUSSION

Structures such as the thick-walled root hairs under discussion are commonly associated with xerophytic conditions, and at first it was thought that perhaps desiccation would explain their presence. When they were found in various types of habitats including bottomland forests, however, and when they were found deep in the soil as well as in the superficial layers, the idea that their presence could be explained as due directly to desiccation was quickly dispelled. However, *Gleditsia triacanthos* has a rather wide specific range of tolerance with respect to habitat. In Illinois it occurs most commonly in bottomland forests along streams, where it is a characteristic tree. But it is also a characteristic tree of the dry barrens of Kentucky and of dry hills elsewhere. For this reason, it is the opinion of the writer that these thick-walled hairs, together with the thorns which are also so characteristic of this species, are relics of a time when the tree grew only under more arid conditions. (It should be added here that *Gleditsia triacanthos inermis*, which lacks the thorns, produces thick-walled root hairs as abundantly as the species). In the case of Gymnocladus and Cercis, both of which have a lesser specific range of tolerance with respect to habitat than has Gleditsia, there have probably been greater constitutional changes during the course of evolution, and they have retained the characteristics due to an arid climate to a much lesser extent.

As previously stated, my observations indicate that in general, except when broken off by growth movements of the roots in the soil, the root hairs remain for as long a time as the rest of the epidermis. In some cases this may be only a few weeks while in other cases it may be several months. McDougall[1] has shown that the roots of trees grow at any time during the year when they can absorb a sufficient amount of water. Some growth would take place, therefore, and some root hairs would be formed late in the growing season. These would undoubtedly persist through the winter and into the next year until such time as there was sufficient growth to rupture the epidermis and finally cause it to be cast off. Indeed, it is not improbable that in some cases these hairs could rightly be spoken of as perennial.

Harrison and Barlow[2] state that *Gleditsia triacanthos*, *Gymnocladus dioica*, and *Cercis canadensis* never have root nodules (bacterial) but that mycorrhizas are always present on these species. I have never been able to find mycorrhizas on any of the leguminous trees, and it is my opinion that the roots bristling with thick-walled root hairs were mistaken by Harrison and Barlow for mycorrhizas. The absence of both root nodules and mycorrhizas from the roots of these trees is probably to be explained by the fact that the walls of the root hairs become thick and hard so quickly that the parasitic organisms are unable to gain an entrance. It will be recalled that the three trees under consideration all belong to the subfamily Caesalpinioideae. The native species of Cassia, the only other genus of this subfamily represented in our flora, are all herbaceous. They produce root nodules, and so far as I have examined them they do not produce thick-walled root hairs. *Robinia Pseudo-Acacia*, the common locust, belongs to the subfamily Papilionoideae. It also produces nodules and does not have thick-walled root hairs.

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[1] McDougall, W. B. The growth of forest tree roots. Amer. Jour. Bot. **3**: 384–392. 1916.

[2] Harrison, F. C., and Barlow, B. The nodule organism of the Leguminosae—its isolation, cultivation, identification and commercial application. Centralbl. Bact. **19**: 264–272; 426–441. 1907.

SUMMARY

1. The root hairs of *Gleditsia triacanthos* become thick-walled and brown in color within a few days after they are produced. This takes place regularly in all sorts of habitats.

2. These thick-walled root hairs persist as long as the root epidermis, whether this be for a few weeks or for several months, unless they are accidentally broken off by root movements in the soil.

3. The root hairs of *Gymnocladus dioica* and *Cercis canadensis* sometimes become thick-walled and brown, but this phenomenon is not nearly so characteristic of these two species as it is of *Gleditsia triacanthos*.

4. The thick-walled root hairs are considered xerophytic structures and are believed to be relics of a time when the species which possess them grew only under xerophytic conditions.

5. The trees which have thick-walled root hairs produce neither bacterial nodules nor mycorrhizas. This is probably due to the inability of the parasitic organisms to enter the roots through root hairs with thickened walls.

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